PATTERN DEVELOPMENT IN MAMMALS AND BIRDS. III

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PARTIAL ALBINISM IN WILD BIRDS

In birds under natural conditions of wild life partial albinism is fairly common. Lists of species of which albinistic specimens are known were published by Ruthven Deane (1876, 1880) some years ago, and by others. Scattered instances are in all the bird journals or magazines of general natural history. In most cases in which the white markings are clearly defined against the pigmented parts of the plumage, these may be referred to their particular primary breaks between the several areas of pigment formation. In other cases the pigment reduction is of the diffuse type, tending to form spots.

A few instances follow in which the several primary patches have been observed in wild birds, either as accidental marks or as permanent parts of the pattern.

The Crown Patch.—In 1908, a pair of robins nested near Lowell Park, Cambridge, one of which showed a partial separation of the crown patch, through the presence of a white band, as broad as the eye's diameter, passing from one eye around the back of the head to the other eye. In the *Wilson Bulletin* (Vol. 2, p. 45, 1908) W. E. Saunders records the capture of two robins each with a white collar about the neck, probably marking the separation of the neck patches from the shoulder patches. Coues (1878) records a brood of *black* robins at St. John's, N. B., one of which was kept in captivity by the late G. A. Boardman. In September, after moulting, it was still pure black, except for white wings and tail, which seems to indicate an areal restriction of the shoulder and rump patches, though the pigment, where

produced, must have been superabundant. Ward (1908) has described a case of a black robin becoming albinistic and reviews a number of such cases. The ability of the same feather follicles in different moults to produce feathers with different sorts or amounts of pigment is thus evidenced and has lately been carefully studied by Pearl and Boring (1914) in the hen.

In addition to the case of the robin above mentioned, the white line marking off the crown patch from the ear patches is sometimes found abnormally in other birds. Thus Sweet (1907) records two slate-colored juncos (*Junco hyemalis*) taken in March, 1903, at Avon, Maine, in which there was a white line above the eye, and the black throat patch was absent, owing no doubt to the ventral restriction of the neck patches, as often seen, for example in pigeons. Maynard[1] figures the head of a young female black-poll warbler (*Dendroica striata*) in autumn, showing an inclination to assume a white superciliary stripe. I am convinced that this mark so common in many birds, is merely a development of the primary break marking off the crown patch from the ear patches so that it has become a permanent part of the pattern.

The failure of the crown patch to develop at all, as is sometimes the case in the domestic pigeon, results in a white-crowned bird. In the West Indian *Columba leucocephala,* exactly this modification has taken place and the entire top of the head is permanently white. The same condition is found in sundry other genera, including a humming bird, a heron, and others. It would be interesting to discover by experiment if it were not easier to produce a definite white marking through selecting for the non-development of a certain patch or patches, than to try to restrict a certain pigment patch to definite bounds as in the experiments of Dr. MacCurdy and Professor Castle (1907).

The crown patch as a separate unit in pigmentation, is often of a different hue from the surrounding patches.

[1] "Birds of E. North America," 1896, p. 585.

Thus in the case of the terns, the black-capped chickadee, the black-crowned night heron, and other birds, a black crown patch is noticeably marked off.

The Ear Patches.—The ear patches in birds are small, yet often specially marked out by white boundaries, which are permanent parts of the pattern. Yet there is no doubt but that the acquisition of such white boundaries is a derived character. It is common for the ear patches to be colored differently from the surrounding parts, forming as in some species of tanagers a black auricular area contrasted with the blue of the head and neck. Of particular interest in the present connection, however, are those cases in which a pigmented ear patch is more or less clearly marked off by a white line above it or below, or both. The superciliary stripe, so common in birds, is of course a development of a primary break above the patch, separating it from the crown patch. Where the stripe is narrow it is hard to say which patch has begun to be restricted, though often no doubt both are more or less involved. Thus the Garganey teal has a very wide white eye stripe, and in other species of ducks the whole side of the head may be white, indicating much greater restriction of pigment formation in contiguous patches. A beautiful example of the development of a white stripe at the *lower* border of the ear patches is found in the Inca tern, in which a line of white feathers runs from just above the gape along the lower side of the auricular patch and separates it from the dark throat. But not only is the white line developed, but the feathers composing it are specially elongated and recurved, as if the mark were one of particular decorativeness. The dark ear patch is noticeable in many hawks, separated above and below by white areas, as in the duck hawk and the osprey, though differing in the size of the white areas.

An instance in which the white line separating the crown patch from the ear patch, is even now in course of becoming established as part of the permanent pattern,

is afforded by the common guillemot (*Uria troille*) of the northern Atlantic. The other related species of the genus have the head and neck uniformly pigmented, but in *U. troille* a considerable proportion of specimens show a narrow white eyebrow and a postorbital line, in exactly the situation of the stripe in the albino robin previously noted, though not so broad nor so extended. Birds so marked were formerly considered a distinct species—the ringed murre (*Uria "ringvia"*)—or perhaps a plumage of *U. troille,* and much effort has been made to determine their exact status. Both plumages are found in the same colonies and the two sorts of birds are known to have mated together (Müller, 1862). Verrill estimated that about 40 per cent. of the nesting birds he saw on the Labrador coast were of this variety, but this is probably a rather high estimate. I am convinced that the true explanation of this puzzling variation is that incipient albinism has gained a foothold, of such nature that areal restriction of the ear or crown patches is developing, so that a white line results between them. In the crested auklet (*Æthia*) a member of the same family, of the Pacific Coast, such a line has become fixed so that it now forms a characteristic mark of the species. In the case of the "ringed murre," I should expect to see the eye stripe in the young as well as in the adult stage of those individuals which are to have the mark—in other words it is a permanent trait. No doubt the heredity of this white stripe is of some definite sort, and if a recessive character, it may nevertheless in time become common to an increasing number of birds, as this is a colonial species and the possibility of inbreeding is thus increased.

The Neck Patches.—In birds the neck patches extend forward from the breast to meet the crown patch at the occiput and the ear patches at the sides of the head, thence ventrally to include the throat and chin. A study of albinistic pigeons, as previously noted, indicates that the neck patches are two separate areas of pigmentation,

one on each half of the part covered, with an ultimate center at the base of the neck, usually the last spot to remain when the area is much reduced.

In albinistic individuals, that is, those in which restriction of the pigment areas has taken place, the neck patches are usually first reduced at the upper part of the throat, so that a white patch appears from the chin to upper throat, as commonly seen in street pigeons; in others, however, the restriction may be at the posterior end of the patch, so that a white ring develops at the base of the neck.

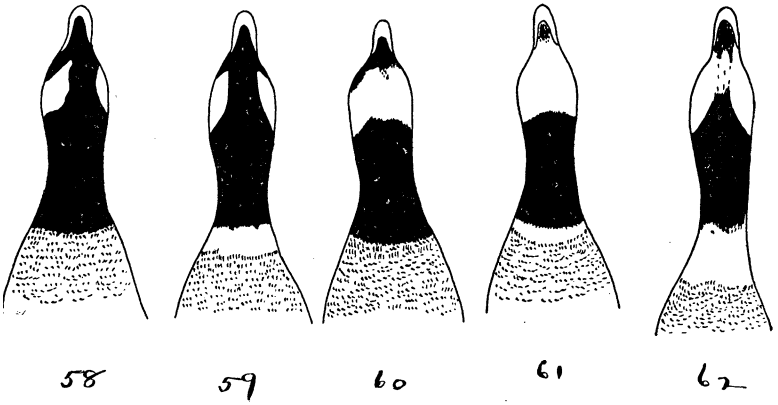
In many birds the neck patches have been much developed as characteristic pigmented areas. Two general categories may be here distinguished: (1) those in which the neck is rather uniformly colored all about, and (2) those in which the ventral portion is heavily pigmented and the dorsal portion much less so. In the latter belong such birds as the black-capped chickadee (*Penthestes atricapillus*) with a black throat but a pale neck. So, too, the golden-winged warbler (*Vermivora chrysoptera*). In this latter category it is probable that a second factor is present, comparable to that producing a centrifugal type of pigmentation in mammals, such for example as in the Himalayan breed of rabbit, which has the end of the nose and the feet black-pigmented, contrary to the usual rule of normal areal reduction where the extremities are the first to become white. That this is a separate category from a physiological standpoint is indicated by its behavior in heredity as worked out so admirably by Faxon (1913) in the case of the Brewster's warbler. He discovered that the black throat as present in the golden-winged warbler is recessive in the cross with a related species, the blue-winged warbler (*Vermivora pinus*), a yellow-throated bird. The offspring of this cross have white throats,—the so-called *V. leucobronchialis*. The black throat patch may be evidence of "centrifugal" pigmentation as defined farther on (p. 53). The essential bilaterality of such a throat patch is

further shown by the fact that one half only may be present as in the golden-winged warbler recorded by Dr. C. W. Townsend (1908).

The first category, in which the neck is uniformly pigmented is illustrated by many of the duck tribe, and probably involves the normal primary patches only. The primary patches are usually restricted first antero-ventrally producing a white throat. Often this is carried dorsally so as to form a white ring around the upper part of the neck by the separation of the neck patch from the crown and the ear patches. Again, if the neck patches are restricted posteriorly a white ring is formed at the base of the neck, a common permanent character in many species. The peculiar little goose-like bird—*Nettapus,* of India—has developed this type of marking so that its white neck is encircled by a narrow black ring, and the Labrador duck (*Camptorhynchus*) has a nearly similar mark (Fig. 57). Other ducks, *e. g.,* the mallard, have the white ring at the base of the neck, only.

In an interesting paper on the geese occurring in California, Swarth (1913) has pointed out that in the cackling goose (*Branta c. minina*) there is much variation in the amount of white on the head and neck. Figs. 58 to 62 are traced from a series of photographs illustrating this paper and show the throats of five specimens. The wide range of variation in these specimens indicates to my mind that this goose is in process of reducing the neck patches, and thereby developing a white collar, such as is present in the mallard, and perhaps also a white throat. The usual condition seen in *Branta canadensis* and in so-called normal specimens of *B. c. minina* is seen in Fig. 58. The white cheeks have been developed long ago in the history of the species, in part perhaps by the depigmentation of the ear patches. Now a second change is taking place in one of its subspecies. Thus in Figs. 59, 61 and 62, the neck patches have been reduced posteriorly, a varying amount in each case. In Figs. 60, 61 and 62 these patches have been restricted anteriorly pro-

ducing a white throat, and as sometimes in the pigeon, imperfectly, so that a little island of pigment is cut off just at the chin. It is also obvious from these figures, that reduction may take place either at one end or the other, or at both ends in different individuals. The ultimate development of this line of reduction will produce



FIGS. 58–62. VARIATIONS IN THE DEVELOPMENT OF THE NECK PATCHES IN THE CACKLING GOOSE (after Swarth).

the narrow black collar seen in *Nettapus* previously mentioned. It is worth noting also that in this goose the limits of the neck patch are by their black color sharply defined posteriorly from the gray of the breast which is pigmented from the shoulder patches.

The Shoulder Patches.—The shoulder patches appear to center near the base of the wing, and in reduction produce white remiges, such as appear in a domesticated race of guinea fowl, as well as a white breast. The domesticated guinea fowl often shows this white area in the midline of the breast as the pigment areas fail to spread ventrally. In the normal pattern of wild birds, however, white wings are seldom seen except among certain sea birds. White wing patches are often developed, but these are frequently only bars on pigmented feathers as in the goat-suckers. Probably among small land birds much white in the large wing feathers is a disadvantage,

and so not much developed. It is noticeable that white patches in the wing are often of such a nature that they are concealed through the folding of the wings when the bird is at rest. This accords with my belief that while in flight the bird is unavoidably conspicuous by reason of its motion, and that white patches showing at such times add little or nothing to the disadvantage. In the hairy and the downy woodpeckers (*Dryobates*), a white stripe down the back is developed as part of the pattern, and no doubt as in many mammals, marks the separation between the pigment areas of opposite sides. Centrifugal pigmentation is seen in some species as the kittiwake in which the *outer* primaries are black.

The side patches are commonly continuous with those of the shoulders, and when ventrally restricted, give a white abdomen. Their median separation dorsally, is seen in the hairy and downy woodpeckers as above noted. I have not studied any special developments of these areas, and they are commonly small.

The Rump Patches.—In birds as in mammals the two rump patches pigment the posterior extremity of the body. Their ultimate centers are dorsal and so close together that it is much less common for them to be separated medially than to be restricted laterally. With a slight areal reduction, a separation takes place between them and the side patches dorsally, so that a white area on the rump results. Often this white area represents doubtless a slight restriction of both sets of pigment patches which by drawing farther apart increase the white area along the lower part of the back. In the domestic pigeon much variation may be found, from a condition in which the lower back is wholly pigmented to one in which it is mostly white. The primary break which causes this white patch has been much developed in many groups of birds as a particular mark in the pattern. In many species it is simply of a paler hue than the surrounding parts as in the yellow-rumped warbler (*Dendroica coronata*) or the pine grosbeak (*Pinicola*).

In others the tendency to albinism thus expressed has gone farther so that a pigmentless spot is formed. This white rump patch is present in many unrelated groups of birds in which it has independently arisen through parallel development. Thus it is seen in many of the smaller petrels, in the palm swift, the flicker woodpecker, the white-rumped and other sandpipers, the white-rumped shrike, the European house martin and others. The tail feathers are pigmented by these patches, and among various species show many steps in the process of pigment reduction. As in the domestic pigeon, occasional albinistic individuals show white outer tail feathers, in accordance with the rule that the first pigment reduction takes place at those parts of the primary areas that are farthest removed from the pigment centers. I have seen a white outer tail feather in wild specimens of song sparrows and Lincoln's sparrow and it is occasional in other species. In others again this mark has become developed and fixed as a species character. Thus in the bay-winged bunting (*Poœcetes gramineus*) there is a single white outer feather on each side, in the junco (*Junco hyemalis*) there are two. A white central tail feather is much rarer, but a pure white tail is found occasionally as in the hummingbird, *Leucuria phalerata,* the bald eagle and certain gulls, due to the permanent reduction of the pigment area of the rump at this extremity. I once examined an albino ruffed grouse (*Bonasa*) which was entirely white except for a single feather among the upper tail coverts at the left side of the rump. This blemish in the otherwise pure white bird seemed inexplicable to those who examined it with me, but it merely represents the last remnant of the left-hand rump patch, still persisting though all the other pigment centers were inactive.

It is very interesting that the white rump mark, so commonly found in unrelated groups of birds, is one which is conspicuous in flight only, and the same is true of many of the white tail marks, such as outer white

feathers that disappear when the tail is shut. This points to the conclusion that the development of a white mark which is ever conspicuous is allowed in nature in such cases only where it may be no detriment to the species through rendering it too conspicuous by contrast. Thus the bald eagle or the black-backed gull have nothing to fear from such a banner mark. For small weak-flying birds, however, the case may well be different. Yet even these often show much white and I believe that it would be possible for a species in its phylogeny to develop more and more white if at the same time its habits of watchfulness or other actions developed equally to counteract any disadvantageous result that might accompany the increase. No doubt also a psychic factor is involved, comparable to what among ourselves we call "fashion." Thus a change in action or dress which departs too far from the accustomed appearance is apt to be disliked at first, though in time it may if persisted in, be tolerated and at length accepted. In the development of white markings, for example in the feathers of the tail, it seems likely that a series of small steps must have been made rather than too great and sudden changes. So in the rock pigeon the white of the tail is limited to the outer vane of the outer tail feather. In the turtle dove the outer vane of the outer feather, and the entire tips of the four outer feathers are white. The next step would be to develop an entirely white outer feather and then two (as in the passenger pigeon) and so on. In the sparrows similar steps are shown by the lark sparrow (*Chondestes*) in which the tips only of the outer feathers are white, the bay-winged bunting which has practically all the outer feather white, and a little of the tip of the second, the junco with two outer feathers and part of a third white. No doubt steps such as these must have been passed through by many white-tailed species.

It is difficult to say how disagreeable to their normally colored neighbors, albino birds may be. I have seen an albino robin in the fall of the year with a flock of other

robins and a white-spotted bee-eater with a flock of its brethren, in both cases wholly at peace. This of course was in flocking time when the social spirit is strong. The song sparrow (*Melospiza*) with white outer tail feathers, previously mentioned, was attacked and driven off by another song sparrow. In the *Journal of the Maine Ornithological Society* (Vol. 6, p. 48, 1904), C. H. Clark writes of a pair of albino eave swallows (*Petrochelidon lunifrons*), at Lubec, Maine,

> among a large colony of the common ones who seemed greatly annoyed at the albinos' presence and fought with them until they finally killed one . . . or rather injured it so badly that it died soon after.

I also have a note of a white robin at Montclair, N. J., which in early July, 1909, was seen to be much beaten and driven about by another robin and eventually flew at full speed against a tree and was killed.

CENTRIFUGAL COLORATION

In addition to the primary pigment patches which I have discussed at some length, and the speckled condition or "English" marking, there is, as I have already intimated, a third condition in which pigment is developed at the extremities or points. It may be called a *centrifugal* type and is almost the reverse of the *centripetal* or "primary-patch" class.

The two latter types of pigmentation may both be found in the same individual, but ordinarily this is not evident except in cases where the primary patches are somewhat restricted in area. It then may become apparent that pigment is present at exactly those points where, in the centripetal type of coloring, it is first to be lacking. Moreover it persists strongly, even though the primary areas are much reduced or largely absent. Curiously this sort of pigment seems almost always to be *black*. Apparently centrifugal pigmentation does not occur in all species. I have never seen any trace of it in dogs. In the house cat it is frequent, however. Thus in Figs.

18 and 19 it appears at the end of the tail. In the former figure the sacral patches are much reduced, though present, and together spread nearly half the length of the tail. The terminal half, or less, of the tail, however, is dark-pigmented, and a break occurs between the two sorts of markings, due to the failure of the centripetal patch to spread so as to unite with the centrifugal area. In Fig. 19 the sacral patches have wholly failed to develop but the centrifugal patch still covers the distal half of the tail. Possibly the dark heel marks in Fig. 16 are patches developed in the same way. In the house cat, a dark or "smutty" nose is often present in contrast to an otherwise white face, or with the ear patches only slightly reduced. In the breed of rabbits known as "Himalayan," the centrifugal pigmentation remains, though the centripetal markings have disappeared, so that it is pure white except for the black nose, ear tips and toes. No doubt, however, it would be possible for the two types of pigmentation to appear in a single individual. This is suggestive of the winter phase of the Arctic hares, in which the black ear tips contrast strongly with the otherwise white pelage. The physiology of the process whereby certain animals acquire a white winter coat is not yet fully worked out. It is curious that in occasional *melanistic* individuals of the eastern varying hare, the black color is retained throughout the winter, instead of being replaced by white—again a persistence of *black* pigment. In dappled gray horses a black patch sometimes appears on the bridge of the muzzle, usually the first place to show white in the restriction of centipetal pigmentation. The feet may also be black. Among certain antelopes a black muzzle mark is similarly present, and in Hunter's antelope (*Damaliscus hunteri*) a white border partly surrounds such a mark. This, I believe, is due to a slight restriction of the ear patches, sufficient to prevent them from reaching the muzzle, and of about the same nature as seen in the blesbok (*Damaliscus albifrons*) in which, through the *absence* of a centrifugal nose patch, the entire

front of the muzzle is white. The white chevron on the muzzle of several antelope (*Strepsiceros, Taurotragus*) is probably the result of a similar restriction of ear patches combined with a centrifugal nose patch, leaving a white line between. The black dorsal stripe seen in many mammals and the black tail tip are probably manifestations of centrifugal pigmentation. The latter mark is common in stoats (*Mustela*) and among those that change to a white coat in winter, as the ermine, the tail tip still remains black. In sundry other genera, as *Genetta,* a black tail tip is part of the normal pattern.

In their paper on albinistic negroes, Simpson and Castle (1913) published some highly interesting photographs of "piebald" individuals. In four persons of one negro family the hair over the median part of the head from the occiput to forehead is pure white, as though due to a restriction of the aural pigment patches. In addition, more or less of the median area of the back, as well as the hands (including much of the forearms) and feet (including the lower part of the ankle) are pigmented. These latter areas may represent centrifugal pigmentation, but it should be noted that this is present in the dermis. Possibly there is a close relation between dermal pigment and that produced in the centrifugal style of pigmentation.

Among birds, the black of the outer tail feathers of the ptarmigan (*Lagopus*) may be comparable. A black area is also sometimes present on the middle of the throat, or as in certain gulls the outer primaries may be black.

This form of pigmentation is not found universally and the conditions governing its appearance are unknown, though its heredity in the "Himalayan" rabbit has been somewhat studied by Professor Castle.

SUMMARY

The principal points of this paper may be summed up as follows:

1. In mammals and birds that normally are com-

pletely pigmented, there are certain definite points of the body from which as centers the tendency to develop pigment in the epidermal structures may become less and less. Outward from each of these centers pigment formation spreads to include very definite areas which in wholly pigmented animals overlap slightly at their borders or are at least contiguous.

2. A reduction in the area covered by any of these primary patches results in a white mark at the line of junction of two contiguous color patches, where no pigment is produced. These white marks between the primary patches are spoken of as primary breaks.

3. Through a study of the breaks in pied individuals of domesticated species of mammals and birds, the boundaries of the primary patches have been determined. These are homologous in the two groups and subject to a certain amount of variation in different types. They are: a median crown patch unpaired, and five paired patches on the opposite sides of the body, which are named from the general areas they cover, the ear, neck, shoulder, side and rump patches. Their limits are more precisely defined under the different species treated.

4. These patches are physiologically independent of each other and may be differently colored in the same individual.

5. Pied patterns among many wild species have been brought about through the areal reduction of these pigment patches in a definite way so that the white markings resulting as breaks between the reduced patches have become fixed and form a permanent part of the normal pattern.

6. In several wild species this development of white markings is shown to be even now taking place, but the amount of pigment reduction is still fluctuating so that the white markings vary much in extent with different individuals.

7. The development of such white markings takes place probably by little and little, so that the departure from

type is not so great as to arouse antagonism against the varying individual on the part of others of its species. Also, the gradualness of the change allows the species to become accommodated to any disadvantage that might concomitantly arise.

8. The converse of this centripetal style of pigmentation is present in many species, and results in pigmentation (commonly black) at the extremities or along lines where primary breaks occur in the centripetal form, namely at the tip of the nose, ears, tip of the tail or the toes; possibly the black dorsal stripe is due also to centrifugal pigmentation. Patterns may develop as in certain antelopes by a white break between patches of the two types.

In conclusion, I wish to express my indebtedness to Professor W. E. Castle for much helpful criticism and advice, and to the Museum of Comparative Zoology for permission to make record of specimens in its study collection.

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